The Hand Skeleton of *Notharctus tenebrosus* (Primates, Notharctidae) and Its Significance for the Origin of the Primate Hand

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ABSTRACT

Recently discovered hand and wrist remains of *Notharctus tenebrosus,* a mid-Eocene adapid primate from North America, are described and compared with the hand skeletons of extant and fossil primates. The carpus of *Notharctus* resembles that of extant pronograde lemurids and platyrrhines in having a relatively tall pisiform body, radioulnarly expanded capitate head, and radioulnarly expanded distal triquetral articular surface. The wrist of *Notharctus* differs from that of the extant primates examined in having a very narrow (radioulnarly) trapezium and transversely broad trapezoid. Functional inferences derived from these osteometric comparisons suggest frequent arboreal, quadrupedal postures for *Notharctus.* The carpal morphology of *Notharctus* is closer to that of *Smilo-* *dectes* than that of *Adapis.* Relative lengths of the *Notharctus* hand, metacarpus, and phalanges are similar to those of extant *Tarsius,* and relative thumb length of *Notharctus* is most like that of *Tarsius* and *Microcebus* among extant primates. This specimen resembles the hands of many living strepsirhine primates in having a very long fourth digit (ectaxony). Hand comparisons between *Notharctus,* extant primates, and early Tertiary adapiforms indicate that a tall pisiform body, robust triquetrum, short metacarpals, long phalanges, and a moderately elongate thumb are probably primitive for the order Primates (= euprimate morphotype). These features suggest that the last common ancestor of primates was an arboreal, pronograde, grasp-leaping form.

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INTRODUCTION

The limb skeleton of *Notharctus tenebrosus* has been known in considerable detail since the publication of Gregory's (1920) classic monograph. Unfortunately, only four carpal bones were available to Gregory (1920), making the hand and wrist the most poorly known anatomical region of *Notharctus*. Recent American Museum of Natural History paleontological expeditions to the Bridger Basin, Wyoming, have yielded several complete craniodental and postcranial specimens attributable to the middle Eocene primate *Notharctus tenebrosus*. Among these materials are forelimb remains that preserve the hand virtually in its entirety—all ten carpals, five metacarpals, five proximal phalanges, several intermediate phalanges, and five terminal phalanges are represented. This new carpal material provides knowledge of a heretofore unknown anatomical region of perhaps the most well-known Paleogene primate. These specimens represent the most complete hand skeleton known for any early Tertiary primate, and therefore provide important insights into the early evolution of this structurally and functionally complex region.

Description of this new fossil material is especially timely given the recent interest in the functional and evolutionary morphology of the primate hand and wrist (Beard and Godinot, 1988; Beard et al., 1988; Godinot and Beard, 1991; Godinot, 1992; Jouffroy et al., 1991; Preuschoft and Chivers, 1993, and references therein; Hamrick, 1996). These studies have addressed both the functional (Godinot, 1992; Godinot and Beard, 1991; Jouffroy et al., 1991) and phylogenetic (Beard and Godinot, 1988; Beard et al., 1988) implications of interspecific variation in early primate hand morphology. Conclusions regarding the former have been limited by a lack of quantitative data for a broad sample of extant taxa, whereas an understanding of the latter has been constrained by a dearth of relevant fossil evidence.

The primary objectives of this study are to (1) describe this fossil hand, (2) reconstruct its functional conditions, and (3) use these data to test hypotheses regarding bony hand features regarded as primitive for the order Primates.

MATERIALS AND METHODS

LOCATION AND GEOLOGY

The specimen discussed here is American Museum of Natural History (AMNH) specimen 127167, a partial skeleton of *Notharctus tenebrosus* discovered in July of 1988 by Mr. Frank Ippolito and Dr. Eugene S. Gaffney of the American Museum of Natural History. Associated cranial and postcranial elements include the skull, mandible, remains of the axial skeleton (atlas to lumbar vertebrae), a nearly complete left forelimb and hand, and partial hindlimb. The complete skull and mandible of AMNH 127167 were found associated with the forelimb remains described here, which allow these postcranial elements to be positively identified as belonging to *Notharctus tenebrosus* (Alexander, 1994; fig. 1).

The specimen was quarried in situ (fig. 1) from a light gray-green silt stone in the Black's Fork Member of the Bridger Formation (Bridger B; West, 1976). The discovery site is located on "Butch Hill" toward the northern end of Grizzly Buttes East, approximately 3 km southwest of the outlying butte Turtle Hill and 10 km southeast of Lyman, Wyoming. Field parties from the American Museum of Natural History led by Walter Granger collected in this area between 1902 and 1903, and it is likely that many specimens of *Notharctus* discovered by these early field parties actually came from the immediate environs of Butch Hill.

OSTEOMETRICS AND STATISTICAL ANALYSIS

Linear measurements of the individual carpal elements (table 1) were obtained for AMNH 127167 and a large comparative sample of extant taxa (table 2). Linear carpal dimensions were expressed as shape ratios in order to make direct interspecific comparisons of the carpal features examined in this study. A regional size variable, "carpal size," was calculated as the geometric mean of 13 linear carpal dimensions taken on the distal radius, ulna, and six individual carpal

Fig. 1.   Photograph of AMNH 127167 in dorsal view, as it was discovered in situ.

elements. Each of the linear carpal measurements was then divided by the carpal size variable to create a new shape variable for each individual for each linear dimension. Summary statistics and sample sizes for these shape variables are presented in table 2.

Mean species shape ratios were then log-transformed to create log-shape variables (Darroch and Mosimann, 1985; Falsetti et al., 1993) which were then included in a multivariate principal coordinates analysis in order to investigate phenetic resemblances in carpal morphology between *Notharctus* and the extant primate sample. A minimum spanning tree (MST) was also generated from the average taxonomic distance matrix for the extant sample and AMNH 127167 to further evaluate the level of phenetic similarity between these taxa. Statistical analyses were performed using the NT-SYS (Numeric Taxonomic System of Statistical Programs; Rohlf et al., 1986) statistical software package. Qualitative comparisons were made be-

TABLE 1
Abbreviations and Definitions for Linear Carpal Measurements

Abbreviation	Variable	Measurement
RSL	Radial styloid length	Anteroposterior length of the radial styloid
USTW	Ulnar styloid length	Anteroposterior length of the ulnar styloid
SCW	Scaphoid breadth	Maximum mediolateral breadth of the proximal scaphoid articular surface
LUNW	Lunate breadth	Maximum mediolateral breadth of the proximal lunate articular surface
PISH	Pisiform height	Dorsopalmar height of the pisiform body
TQDW	Triquetral distal breadth	Maximum mediolateral breadth of the triquetral articular facet for the hamate
HAMW	Hamate breadth	Maximum mediolateral breadth of the distal hamate surface
CAPW	Capitate head breadth	Maximum mediolateral breadth of the capitate head
TDW	Trapezoid breadth	Maximum mediolateral breadth of the distal trapezoid surface
TMW	Trapezium breadth	Maximum mediolateral breadth of the trapezium facet for the first metacarpal

TABLE 2
Summary Statistics for Raw Shape Variables
Abbreviations are spelled out in table 1, sample sizes are in brackets, mean values are shown above, and standard deviations are in parentheses.

Species[a]	RSL	USTW	SCW	LUNW	PISH	TQDW	HAMW	CAPW	TDW	TMW
Ii	.44	.71	1.29	.58	1.14	.97	1.3	.47	.72	1.19
[11]	(.11)	(.08)	(.07)	(.09)	(.06)	(.04)	(.08)	(.09)	(.08)	(.10)
Pv	.45	.78	1.31	.80	1.27	.95	1.26	.48	.63	1.15
[16]	(.08)	(.08)	(.09)	(.14)	(.13)	(.08)	(.08)	(.05)	(.07)	(.17)
Lc	.62	.90	1.26	.71	1.20	.98	1.36	.50	.76	.97
[15]	(.08)	(.05)	(.08)	(.13)	(.12)	(.10)	(.06)	(.04)	(.08)	(.10)
Lf	.64	.89	1.23	.77	1.28	1.0	1.28	.50	.71	.96
[17]	(.08)	(.05)	(.09)	(.09)	(.10)	(.09)	(.07)	(.05)	(.06)	(.11)
Vv	.64	.87	1.24	.65	1.46	1.04	1.29	.52	.70	1.06
[18]	(.07)	(.04)	(.07)	(.09)	(.11)	(.05)	(.06)	(.04)	(.04)	(.12)
Oc	.56	.84	1.13	.93	1.24	.92	1.17	.52	.68	1.10
[14]	(.11)	(.06)	(.09)	(.09)	(.14)	(.05)	(.07)	(.08)	(.04)	(.10)
Nc	.59	.54	1.38	1.15	1.0	.89	.96	.55	.69	1.29
[12]	(.12)	(.07)	(.09)	(.07)	(.12)	(.11)	(.09)	(.05)	(.06)	(.18)
Pp	.61	.59	1.39	1.09	1.02	.90	.99	.51	.69	1.29
[13]	(.08)	(.03)	(.22)	(.08)	(.10)	(.08)	(.10)	(.05)	(.08)	(.13)
T sp.	.48	.78	.91	.73	1.95	1.08	1.14	.52	.87	1.10
[5]	(.09)	(.06)	(.10)	(.04)	(.03)	(.04)	(.05)	(.07)	(.06)	(.12)
At	.55	.71	1.12	.79	1.73	1.04	1.18	.56	.65	.98
[4]	(.10)	(.04)	(.10)	(.05)	(.29)	(.08)	(.08)	(.04)	(.02)	(.05)
Ap	.62	.63	1.0	.84	1.62	1.03	1.16	.56	.60	.98
[4]	(.07)	(.10)	(.05)	(.04)	(.07)	(.01)	(.10)	(.06)	(.02)	(.09)
Nt	.42	.77	1.18	.64	1.45	1.12	1.4	.58	.88	.75

[a] *Ii = Indri indri, Pv = Propithecus verreauxi, Lc = Lemur catta, Lf = Lemur fulvus, Vv = Varecia variegata, Oc = Otolemur crassicaudatus, Nc = Nycticebus coucang, Pp = Perodicticus potto, T* sp. *= Tarsius* spp., *At = Aotus trivirgatus, Ap = Alouatta palliata, Nt = Notharctus tenebrosus* (AMNH 127167).
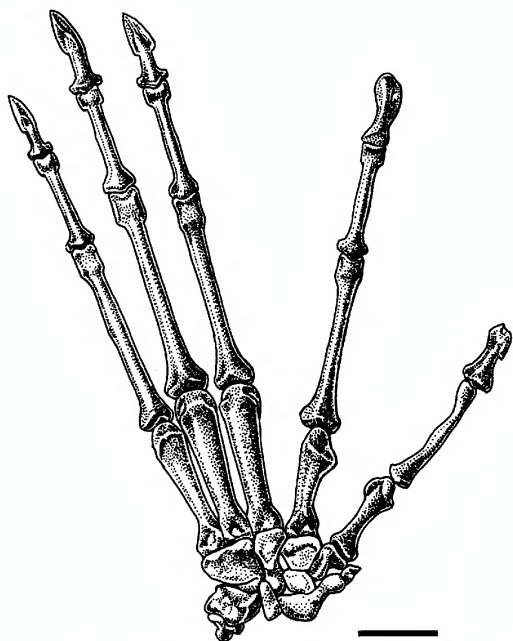
Fig. 2.   Dorsal view of reconstructed hand and wrist of *Notharctus tenebrosus* (AMNH 127167). Scale bar = 1 cm.

tween AMNH 127167 and carpals of *Smilodectes gracilis* (USNM 13251; Smithsonian Institution) and *Adapis parisiensis* (RD 311; Quercy quarry Rosières Deux). Finally, relative hand, thumb, phalangeal, and metacarpal indices were calculated for AMNH 127167, and compared with those of the extant and fossil taxa listed in Jouffroy et al. (1991), Napier and Napier (1967), and Godinot (1992).

DESCRIPTION

SCAPHOID

The scaphoid of AMNH 127167 is from the right hand of *Notharctus tenebrosus,* whereas the remaining carpal elements described here are from the left hand of the same individual. The proximal surface of the scaphoid is convex for articulation with the concave distal radius, and is only slightly wider radioulnarly than dorsopalmarly (= dorsoventrally; figs. 2, 3). On the dorsal and distal side of the scaphoid is a radioulnarly wide, concave facet for articulation with the centrale (fig. 3a). The ulnar and palmar bor-

ders of the distal scaphoid are covered by a flat articular facet for the lunate. The scaphoid tubercle is robust, and projects both distally and palmarly where it contacts the trapezium and forms the most radial margin of the carpal tunnel. A flat facet on the dorsal surface of this tubercle articulates with the trapezium (fig. 3b), and there is a small facet for articulation with the prepollex on the more proximal portion of the tubercle.

CENTRALE

The centrale of *Notharctus* is triangular in dorsal view and striking in its robusticity— the bone is expanded in virtually all directions (fig. 2). The palmar margin of the centrale bears a pointed lip, which curves radially and rests snugly in a groove on the palmar surface of the ulnar capitate, just distal to the capitate head. The distal centrale surface, which articulates with the trapezoid, is triangular in distal view and slightly wider dorsally than palmarly. The dorsal margin of the centrale slopes medially, and is convex for articulation with the concave scaphoid surface.

LUNATE

The lunate is high dorsoventrally and thin radioulnarly, its proximal surface being convex in each direction for articulation with the distal radius (fig. 2). The medial side of the lunate articulates with the triquetrum, and this facet is flat and crescent-shaped. In ulnar view, the distal articular facet of the lunate is deeply concave dorsoventrally so that its dorsal and palmar margins encircle the capitate head at the midcarpal joint. The radial side of the lunate bears a small area of contact for the scaphoid.

TRIQUETRUM

The proximal articular facet of the triquetrum is high dorsopalmarly and narrower radioulnarly, with a bony lip on the dorsal margin that curves over the ulnar facet (fig. 3). The radioulnarly constricted shape of the proximal articular facet indicates that ulnocarpal joint movements were limited primarily to flexion and extension (fig. 3c). Just palmar to this facet is a concave articular surface for the pisiform. The ulnar side of the triquetrum bears a bony, nonarticular process
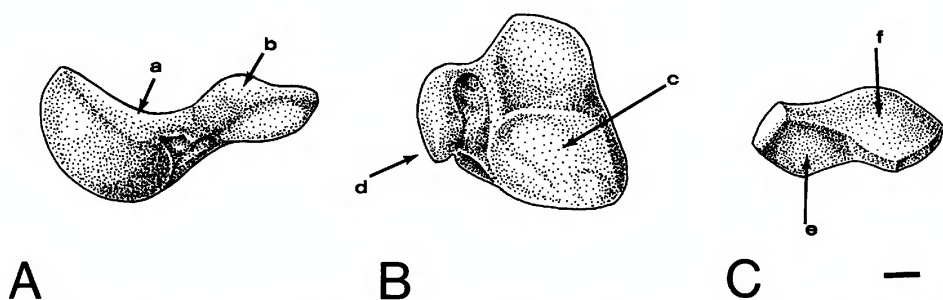
Fig. 3. Bones of proximal carpal row, including (A) scaphoid in dorsal and proximal view, (B) triquetrum in proximal view, and (C) pisiform in proximal view. Arrows point to (a) articular facet for centrale on scaphoid, (b) articular facet for trapezium on scaphoid, (c) articular facet for ulna on triquetrum, (d) insertion site of medial ulnotriquetral ligament, (e) articular facet for ulna on pisiform, and (f) articular facet for triquetrum on the pisiform. Scale bar = 1 mm.

for attachment of the ulnocarpal ligament (fig. 3d). This process is separated from the ulnar facet by a distinct groove. The radial surface of the triquetrum bears a flat articular facet for contact with the lunate, which is widest dorsally and narrower palmarly. The distal articular surface of the triquetrum is concave radioulnarly and flat dorsopalmarly. This facet articulates with the radioulnarly concave proximal hamate facet (the so-called spiral facet) at the midcarpal joint. The triquetrum is large and blocklike and the distal facet is very wide, suggesting that the triquetrohamate articulation was subjected to compressive, weight-bearing loads.

PISIFORM

The pisiform body is robust and is expanded dorsopalmarly, giving it a rodlike shape. Proximally and ulnarly the pisiform bears a concave and radioulnarly wide facet for articulation with the ulna (fig. 3e). The triquetral articular facet is convex and radioulnarly wide, and is located on the distal and lateral side of the pisiform (fig. 3f). The palmar surface of the pisiform body is irregular in shape and rugose for insertion of the m. flexor carpi ulnaris tendon.

HAMATE

The hamate of *Notharctus* bears a proximal spiral facet for articulation with the triquetrum at the midcarpal joint. This facet is directed medially and distally in an oblique orientation (fig. 2). It is convex proximally but becomes deeply concave as it turns pal-

marly in its distal portion (fig. 4A). The ulnar and palmar direction of this facet indicates that, as in many extant arboreal, quadrupedal primates, the midcarpal joint was impacted in a pronated and slightly ulnarly deviated position (Lewis, 1972, 1989). The distal hamate surface bears two articular facets, a larger one for the fourth metacarpal and a smaller one for the third. The hamulus of the hamate is very small and forms a small, blunt process (fig. 4a).

CAPITATE

In dorsal aspect, the capitate head is expanded radially, giving the capitate body a "waisted" appearance (fig. 2). A faint ridge runs proximally and ulnarly off the nonarticular distal portion of the dorsal surface, and this ridge demarcates the centrale articular facet on the radial side from the lunate articular facet proximally (fig. 4b). The centrale facet extends only slightly onto the dorsal capitate surface, whereas the lunate facet covers both the proximal and dorsal surface. The capitate head is smooth on its proximal surface and it is difficult to distinguish any separate lunate and scaphoid articular facets. In radial view the most distal portion of the capitate bears two articular facets: a flat triangular facet for the trapezoid dorsally and a concave facet for the most proximal edge of the second metacarpal palmarly. The trapezoid facet faces proximally, whereas the metacarpal facet faces radially. The most dorsal margin of the capitate extends distally over the metacarpal facet (see also Beard and
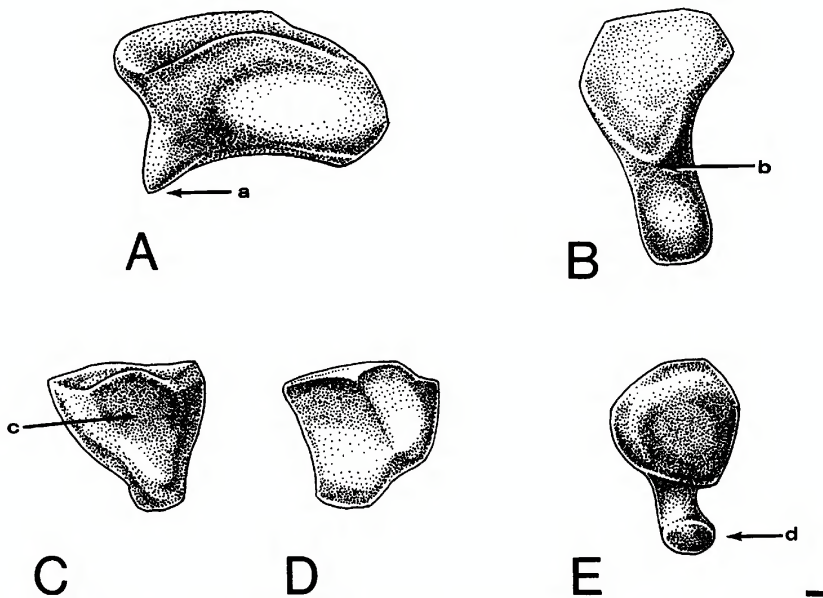
Fig. 4.   Bones of distal carpal row, including **(A)** hamate in medial view, **(B)** capitate in dorsal view, **(C)** trapezoid in proximal view, **(D)** trapezoid in distal view, and **(E)** trapezium in distal view. Arrows point to (a) hamate hamulus, (b) ridge on capitate separating lunate and centrale articular facets, (c) articular facet for centrale on trapezoid, and (d) trapezium tubercle. Scale bar = 1 mm.

Godinot, 1988). The distal surface of the capitate is dominated by two concave facets for the third metacarpal. The radial facet is roughly twice the size of the ulnar, and is tilted somewhat ulnarly. The ulnar side of the capitate articulates solely with the hamate, and bears a large pit for the capitate-hamate interosseous ligament.

TRAPEZOID

The trapezoid is much wider radioulnarly than it is proximodistally (fig. 2). The proximal surface is covered by the articular facet for the centrale, which is convex radioulnarly and slightly concave dorsopalmarly (fig. 4c). The articular facet for the capitate on the most distal and ulnar corner of the trapezoid is crescent-shaped and flat. Because the corresponding facet on the capitate faces somewhat proximally, the distal trapezoid facet for the second metacarpal faces radially, setting metacarpal II toward the thumb and away from metacarpal III (fig. 2). The articular facet for the second metacarpal is deeply concave, with the ulnar facet being larger than the radial facet (fig. 4D). In distal view, the trapezoid is triangular in outline, being

widest on its dorsal edge, narrowing at its palmar region (fig. 4D). The radial side of the trapezoid is covered by a dorsopalmarly convex articular facet for the trapezium.

TRAPEZIUM

The trapezium appears triangular in dorsal view (fig. 2) and it possesses a large palmarly projecting tubercle for attachment of the transverse carpal ligament (fig. 4d). On the ulnar surface of the bone is a large, concave facet for the trapezoid, which is expanded anteroposteriorly and compressed dorsopalmarly. The proximal trapezium surface bears a large, flat facet for the scaphoid tubercle on its ulnar side and a smaller facet for the prepollex on its radial side (fig. 2). The facet for the prepollex is convex, expanded anteroposteriorly, and narrow radioulnarly. The facet for the first metacarpal covers the distal and radial portion of the trapezium (fig. 4D). This facet is saddle-shaped, being convex dorsoventrally and concave radioulnarly. The thumb of *Notharctus* is biaxial, where the trapezium-metacarpal I allows both flexion/extension and adduction/abduction (fig. 4D).

PREPOLLEX

The prepollex is quite large, and in dorsal view resembles an elongate triangle (fig. 2), which "points" palmarly where it receives some fibers from the tendon of *m. abductor pollicis longus.* The dorsal surface of the prepollex bears a small concave facet for the trapezium, which is wider anteroposteriorly than it is radioulnarly. The ulnar surface is covered by a flat articular facet for the scaphoid tubercle.

METACARPALS

The metacarpal length formula is 4 > 3 > 5 > 2 > 1 (fig. 2). The pollical metacarpal is short and stout. The proximal pollical metacarpal surface is wide radioulnarly and high dorsoventrally, with a small process on the most palmar portion of the base. The facet for articulation with the trapezium is sellar, being convex radioulnarly and concave dorsoventrally, indicating that both flexion/extension and adduction/abduction are possible at the pollical carpometacarpal joint. The metacarpal shaft is essentially straight on its ulnar side, but is bowed on the radial side (fig. 2). The facet for the proximal phalanx is narrow radioulnarly but extended dorsoventrally, suggesting a large range of metacarpophalangeal flexion at this joint. This articular facet angles radially toward its palmar margin, which draws the phalanx toward the palm when the joint is flexed. The radial and ulnar tubercles on the metacarpal head are well developed for insertion of the collateral ligaments. These features illustrate that the thumb of AMNH 127167 was capable of considerable flexion at both the pollical carpometacarpal and metacarpophalangeal joints.

The second metacarpal is longer than the first but, like the first metacarpal, it has an extremely stout, robust shaft. The base is rectangular in proximal view, being wider dorsoventrally than it is radioulnarly. There is a concavity on the dorsal and ulnar surface of the base, which articulates with a ridge on the trapezoid. Curiously, the long axis of the metacarpal shaft is turned radially (that is, toward the thumb) at an angle of 30–40° relative to the metacarpal base. This orientation of the shaft spreads digits I, II, and III apart

from one another (fig. 2). The metacarpal head is, like the pollical metacarpal head, quite narrow radioulnarly. The second metacarpal head is, however, also expanded dorsoventrally, which increases the potential range of metacarpophalangeal flexion and extension. Despite the increased length and robusticity of the second metacarpal, the dorsal tubercles on the metacarpal head are not so well developed as those on the pollical metacarpal. The robust second metacarpal and very large trapezoid (fig. 2) suggest that the hand of *Notharctus* may have experienced loads along the long axis of the second digit during quadrupedal locomotion.

Metacarpals III–V differ mainly in the shape of their proximal carpometacarpal articular facets. In proximal view, the base of the third metacarpal is triangular, being wider dorsally than it is palmarly. The metacarpal head is much wider than that of the second metacarpal. The base of the fourth metacarpal bears a concave radial margin, which articulates with a convex facet on the hamate, and also possesses a convex ulnar facet for articulation with a convex corner of the hamate. The head of the fourth metacarpal does not appear to differ significantly in shape from that of metacarpal III. The base of the fifth metacarpal is convex for articulation with a concave facet on the distal hamate surface. The long axis of the fifth metacarpal is directed ulnarly approximately 15° relative to the distal hamate surface, thus spreading the fifth digit away from the fourth. The metacarpal head is quite large relative to the length of the shaft, comparable in overall breadth to that of metacarpal IV.

PHALANGES

The formula for the proximal phalanges is 4 > 3 > 5 > 2 > 1 (fig. 2). They are very elongate and gracile (fig. 2). The bases of these proximal phalanges are extremely high dorsopalmarly but very narrow radioulnarly, bearing only moderately developed palmar tubercles. The great dorsopalmar height of the phalangeal bases suggests that a large range of metacarpophalangeal flexion and extension was possible at these joints. Phalanges II–V have condyles that are elliptical and tilted somewhat anteriorly, evidence of habitually flexed proximal interphalangeal

joints (Hamrick et al., 1995). The flexor sheath ridges are moderately developed and, like those of lemuriforms, are limited to the distal halves of the shafts (Hamrick et al., 1995). The most striking feature of these proximal phalanges is the proximodistal elongation of these elements compared to the metacarpals (fig. 2). The terminal phalanges possess apical tufts that are wider on phalanges I and II, but narrower on phalanges III–V (fig. 2). The second terminal phalanx is also much wider than the terminal pollical phalanx, but of equal length, whereas the ulnar unguals are longer but narrower than the pollical phalanx (fig. 2). All of these terminal phalanges bear somewhat flattened tufts, indicative of nails rather than claws (Dagosto, 1988).

COMPARATIVE MORPHOLOGY

THE CARPUS

Comparisons with Extant Primate Taxa

The principal coordinates analysis of mean species log-shape variables for AMNH 127167 and our sample of extant primates produces four groupings: the lorises and *Otolemur*; the two indriids; the lemurids; and the two anthropoids plus *Tarsius* (fig. 5). These multivariate results demonstrate that the first principal coordinate axis, which accounts for almost 50% of the variance, separates the extant primate sample along a cline of prehensile specialization. The lorises and indriids, which possess a well-developed, divergent pollex, have positive scores on this axis, whereas the lemurs, monkeys, and tarsiers, which lack such a well-developed thumb, have negative scores (fig. 5). AMNH 127167 falls at the low end of factor scores for the first principal coordinate axis, being closest to quadrupedal lemurids, platyrrhines, and *Tarsius* in this respect.

The first principal coordinate axis is most highly correlated with breadth of the triquetrum (table 3): the indriids and lorises have high factor scores on this axis and relatively reduced distal triquetral articular facets, whereas the lemurids and platyrrhines have somewhat lower factor scores and a relatively large distal triquetral surface (fig. 5; tables 2, 3). Primates that load the ulnocarpal and

TABLE 3

Pearson Correlation Coefficients (factor loadings) Between First Three Principal Coordinate Scores and Included Shape Variables

The strongest factor loadings are in bold type. Measurement abbreviations are described in table 1.

	Axis 1 (46.96%)	Axis 2 (21.68%)	Axis 3 (11.61%)
TMW	**.81**	−.13	.11
LUNW	.76	.44	−.03
SCW	.64	−.56	−.11
RSL	.39	−.23	−.78
CAPW	−.20	**.84**	.09
TDW	−.53	−.12	.06
USTW	−.68	−.50	−.45
PISH	−.72	.49	−.13
HAMW	−.77	−.52	−.15
TQDW	**−.87**	.23	.06

midcarpal joints in quadrupedal, weight-bearing postures have a robust triquetrum (Sarmiento, 1988, 1994) and radioulnarly directed triquetral facet on the hamate (Lewis, 1972; Jenkins and Fleagle, 1975; Fleagle, 1977; Fleagle and Meldrum, 1988; Hamrick, 1996a) to support compressive loads transmitted from the ulna to the wrist. The triquetrohamate facet is quite broad in pronograde monkeys and strepsirhines but less so in more orthograde climbers and clingers (table 2). *Notharctus,* like pronograde monkeys, has a very broad hamate facet on the triquetrum (table 2).

The first principal coordinate axis is also highly correlated with relative breadth of the first (pollical) carpometacarpal articular facet on the trapezium (table 3). Breadth of the trapezium reflects relative size of the trapezium-first metacarpal articulation (Hamrick, 1996). Extant primates with a powerful grasping thumb, like indriids and lorises, have an expanded pollical carpometacarpal articulation and hypertrophied trapezium (table 2; Hamrick, 1996a). In contrast, most monkeys lack such an expanded pollical carpometacarpal articulation, and both of the platyrrhines measured here possess a smaller trapezium relative to overall carpal size than most extant strepsirhines (table 2). Note, however, that *Tarsius* has a broader trapezium compared to the platyrrhines (fig. 2). *Notharctus tenebrosus* has a relatively small tra-
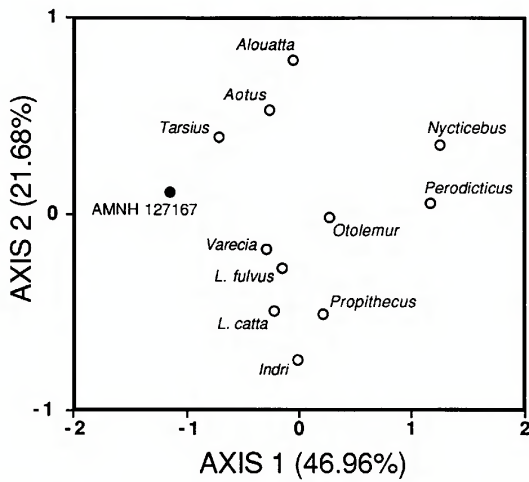
Fig. 5. Bivariate plot of first two principal coordinate axes for the multivariate analysis of logged mean species shape variables shown in table 2.

TABLE 4
Minimum Spanning Tree Distances (MST) Between Taxa

Taxa	Distance
I. indri–P. verreauxi	0.70
P. verreauxi–O. crassicaudatus	0.82
O. crassicaudatus–L. fulvus	0.73
L. fulvus–L. catta	0.32
L. fulvus–V. variegata	0.45
V. variegata–A. trivirgatus	0.87
A. trivirgatus–A. palliata	0.50
O. crassicaudatus–P. potto	1.10
P. potto–N. coucang	0.44
A. trivirgatus–Tarsius	1.12
*A. trivirgatus–*AMNH 127167	**1.37**

pezium given the overall size of its carpus (fig. 2), demonstrating that *Notharctus* is most similar to living monkeys in relative breadth of the first carpometacarpal articulation.

The second principal coordinate axis accounts for approximately 20% of the variance and is most highly correlated with breadth of the capitate head (table 3). Platyrrhines tend to have positive factor scores on this axis (fig. 5), and relatively wide capitate heads (table 2), although there is considerable overlap among taxa for this measure (table 2). A medially expanded capitate head decreases the degree of midcarpal joint curvature (e.g., makes the joint surface flatter radioulnarly) and expands the surface area for contact with the lunate (Lewis, 1972; O'Connor, 1975; Sarmiento, 1988). Hence, a broad capitate head makes the midcarpal joint more stable under weight-bearing loads transmitted from the forelimb to the carpus. Not surprisingly, a broad capitate head is characteristic of habitually pronograde primates (Lewis, 1972; Jenkins and Fleagle, 1975; Sarmiento, 1988; Hamrick, 1993, 1996a). The fact that *Notharctus* has a radioulnarly expanded capitate relative to overall carpal size (table 2) suggests that its midcarpal joint experienced compressive loading during quadrupedal postures.

Minimum spanning tree distances demonstrate that among all of the extant primates included for analysis, carpal dimensions of AMNH 127167 are most similar to those of the owl monkey *Aotus* (table 4). Note, however, that the magnitude of this distance is quite large (table 4), indicating that carpal morphology of this early primate is quite distinctive from that of any of the living primates studied. It is also clear that the carpus of *Notharctus* is quite similar in overall form to that of *Tarsius* (fig. 5). The fact that *Notharctus, Aotus,* and *Tarsius* resemble one another in dimensions of the triquetrum and capitate (table 2) suggests that an expanded triquetrohamate facet and broad capitate head may well be primitive for euprimates as a whole. Functionally, the broad triquetrum and expanded capitate head are related to bearing compressive loads at the midcarpal joint (Sarmiento, 1988, 1994; Hamrick, 1996a). This observation implies that tarsiers have a pronograde ancestry and *Notharctus* exhibits some carpal features functionally related to quadrupedal positional behaviors. Therefore, if these features are primitive for euprimates, then they suggest a pattern of habitual pronograde posture in the earliest primates.

Comparisons with Other Eocene Primates

A complete comparative analysis of adapiform carpal morphology is in progress (Hamrick, 1995a, 1996b); however, some preliminary observations are presented here. *Smilodectes* and *Notharctus* both share a tall
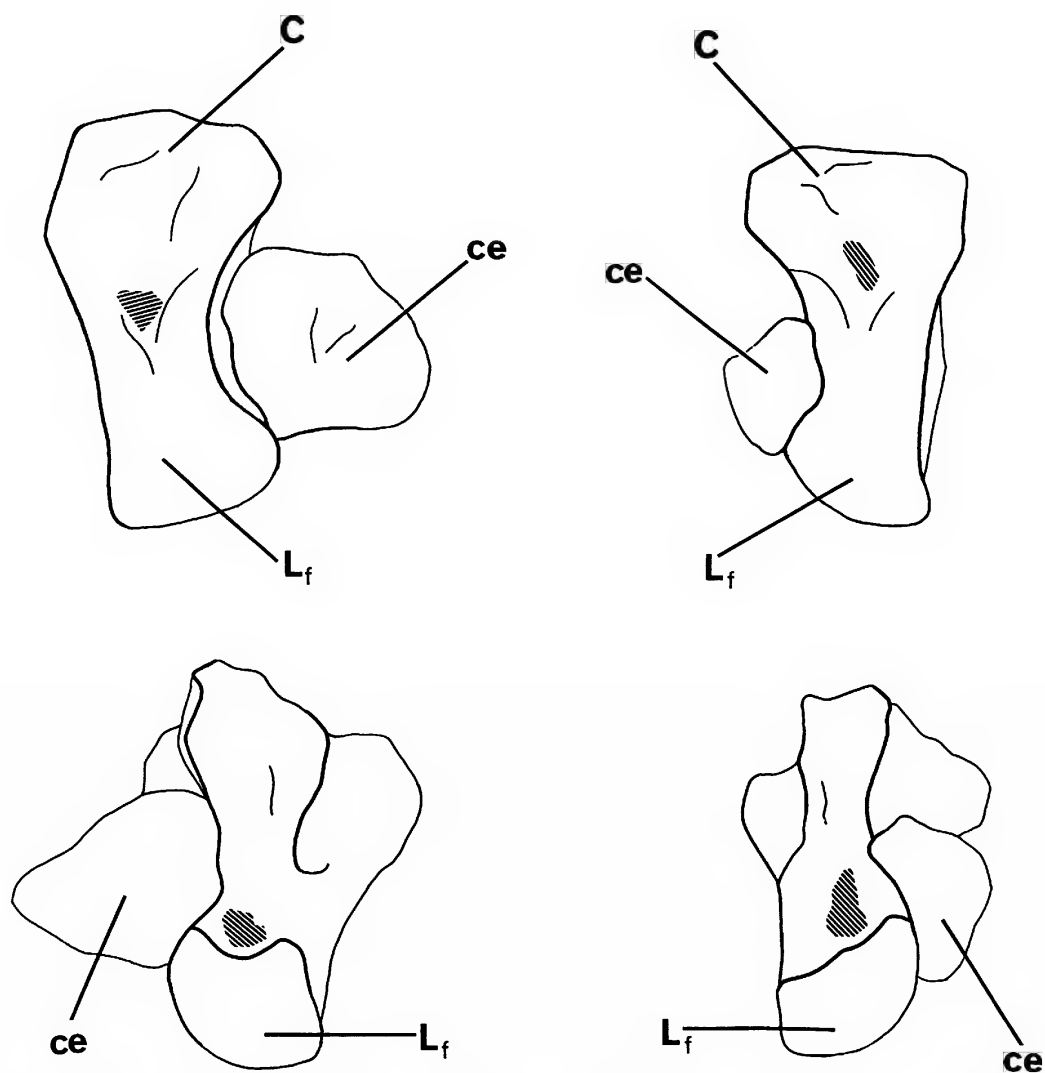
Fig. 6. Articulated capitate (C) and centrale (ce) of *Notharctus tenebrosus* (left; AMNH 127167) and *Smilodectes gracilis* (right; USNM 13251A) in dorsal (top row) and palmar (bottom row) views. L_f = lunate articular facet. Not to scale.

pisiform body and a lunate that is relatively narrow radioulnarly (Godinot and Beard, 1991). The only noticeable way in which these genera differ in proximal carpal joint morphology is that *Smilodectes* has a somewhat shorter tubercle on the scaphoid than does *Notharctus*. This difference may be a consequence of the overall smaller size of *Smilodectes gracilis*. At the midcarpal joint, the most striking difference between these two genera is in the size of the os centrale. The centrale of *Notharctus* is expanded ra-

dioulnarly whereas its radioulnar dimension is more constricted in *Smilodectes* (fig. 6). The centrale of *Smilodectes* is more rectangular in shape, with its long axis directed dorsoventrally, whereas it has a more rhomboidal shape in *Notharctus* (fig. 6). The capitate of AMNH 127167, like the *Notharctus* capitates described by Beard and Godinot (1988), also differs from those of *Smilodectes* in having some distal projection of the dorsal capitate surface. *Notharctus* and *Smilodectes* do not appear to differ in any re-

markable way from one another in morphology of the trapezium, hamate, or other carpal elements.

The proximal wrist joint of *Notharctus* differs from that of *Adapis* in having a proximal lunate surface that is somewhat narrower relative to the proximal surface of the scaphoid. As noted by Godinot and Beard (1991), there is some ulnar extension of the triquetrum's ulnocarpal facet in *Adapis,* whereas it is not expanded ulnarly in *Notharctus* and *Smilodectes.* This contrast may point to a greater range of ulnar deviation at the ulnocarpal joint of *Adapis* (Godinot and Beard, 1991). *Notharctus* and *Adapis* differ principally in relative proportions of the trapezoid and trapezium, and in general morphology of the pollical carpometacarpal articulation (fig. 7). The trapezoid of *Notharctus* is rectangular in dorsal view, being expanded radioulnarly, whereas it is more square-shaped in *Adapis* (fig. 7). The radial side of the trapezium faces somewhat proximally in *Notharctus* and therefore possesses a large articular facet for the scaphoid tubercle (fig. 7). In contrast, the radial surface of the *Adapis* trapezium is turned so far laterally that there is very little articulation with the scaphoid tubercle (fig. 7). In distal view, the pollical metacarpal facet of *Adapis* is crescent-shaped (elongate dorsoventrally and narrow radioulnarly), whereas that of *Notharctus* is rounded and of equal breadth in its radioulnar and dorsoventral directions (fig. 7). Functionally, the shape differences observed between *Notharctus* and *Adapis* are related to midcarpal and carpometacarpal articulations that are relatively expanded in *Notharctus* compared to those of *Adapis.* These differences suggest that the radioulnar expansion of these joints in AMNH 127167 is related to the carpus bearing weight during pronograde postures.

Comparisons and contrasts in carpal morphology between these Eocene taxa and extant primates also allow us to speculate on the pattern of carpal morphology primitive for primates (euprimate morphotype). Beard and Godinot (1988) and Godinot and Beard (1991; see also Dagosto, 1993) concluded that the carpal proportions of notharctines show several features that are primitive for euprimates as a whole. These include: (1) a large pisiform body, (2) a narrow lunate, (3)

a triangular trapezium, and (4) a radioulnarly narrow capitate head. AMNH 127167 possesses most of these features, however the capitate head is expanded radioulnarly (table 2; fig. 4B) resembling *Tarsius* and *Aotus* in this respect (table 2). On the basis of these shared similarities, we conclude that a relatively broad rather than narrow capitate head is primitive for euprimates. A relatively expanded triquetrum is also likely to be primitive for euprimates, as this feature is shared by *Tarsius, Notharctus, Varecia,* and *Aotus* (table 2).

RAY PROPORTIONS

Comparisons with Extant Primate Taxa

The hand of AMNH 127167 represents approximately 35% of the total forelimb length, demonstrating that this specimen has very long hands (fig. 8; table 5). The value of this index for AMNH 127167 is closest to that of *Tarsius* among extant primates (fig. 8). The high value of the hand length index in AMNH 127167 is driven at least in part by the relatively short radius of adapiforms (Rose and Walker, 1985; Jouffroy et al., 1991; Dagosto, 1993). Intrinsic proportions of the *Notharctus* hand are also quite similar to those of *Tarsius* and living strepsirhines. The metacarpals of *Notharctus* are very short relative to total hand length (fig. 8; table 5), whereas the phalanges are quite long relative to hand length (fig. 8; table 5). As Jouffroy et al. (1991) noted, living strepsirhines and tarsiers have short metacarpals whereas the metacarpals of anthropoids are longer relative to total hand length. Our results corroborate Jouffroy et al.'s (1991) hypothesis that short metacarpals and long phalanges are primitive for euprimates, since these proportions are shared by *Notharctus, Tarsius,* and extant strepsirhines. Anthropoids appear derived in having relatively longer metacarpals and shorter phalanges.

The thumb of *Notharctus* is not exceptionally long relative to total hand length (fig. 9A; table 5). It is shorter than that of most platyrrhines and more comparable in relative length to those of *Tarsius, Microcebus,* and certain indriids (fig. 9A). The proportionately longer thumbs of monkeys, compared to those of *Notharctus,* tarsiers, and strepsi-
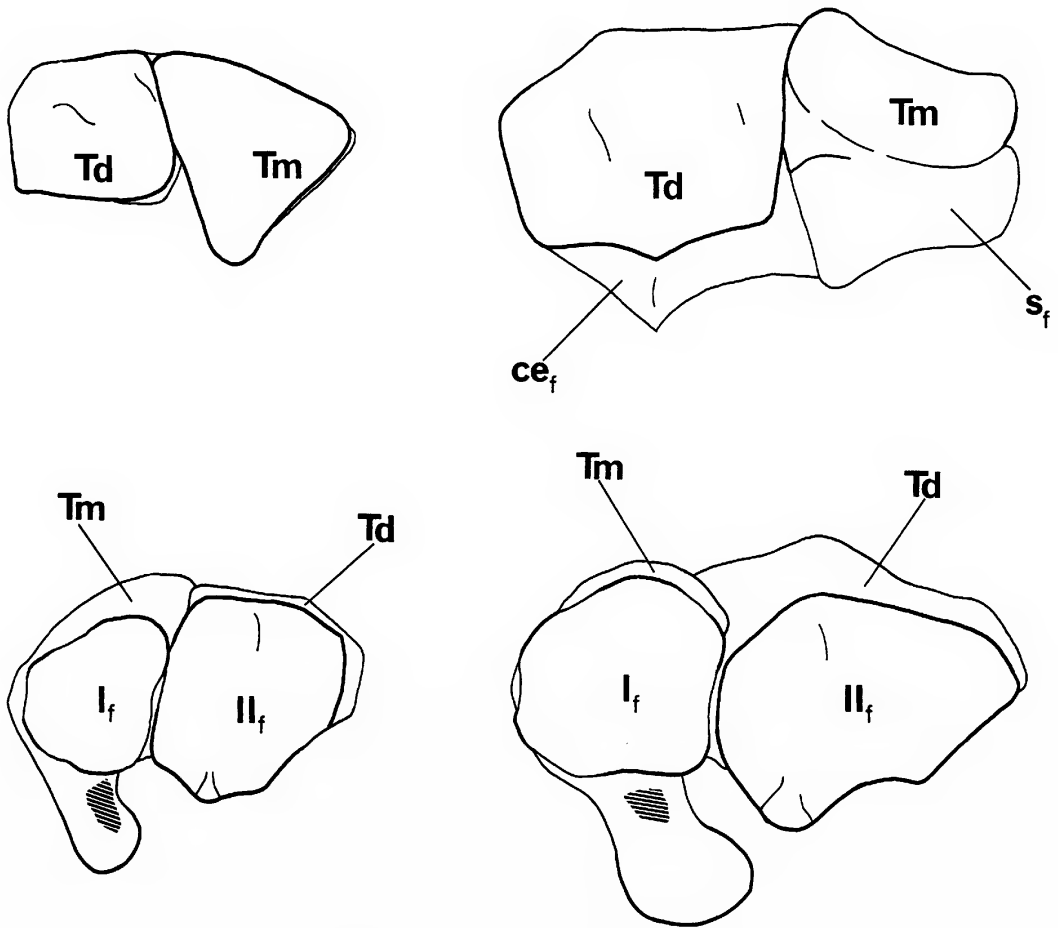
Fig. 7. Articulated trapezoid (Td) and trapezium (Tm) of *Adapis parisiensis* (left; RD 311) and *Notharctus tenebrosus* (right; AMNH 127167) in dorsal (top row) and distal (bottom) views. ce$_f$ = centrale articular facet, s$_f$ = scaphoid tubercle articular facet, I$_f$ = first metacarpal articular facet, II$_f$ = second metacarpal articular facet. Not to scale.

rhines, may be related to greater manual dexterity in monkeys (Napier and Napier, 1967). New World monkeys do, however, possess a pseudo-opposable thumb and whole-hand grasp much like that of strepsirhines (Bishop, 1964; Rose, 1992). Variation in this ratio is therefore probably driven by the relatively shorter hand length of anthropoids (fig. 8) rather than absolutely greater thumb length. The ratio of first metacarpal length to third metacarpal length in AMNH 127167 is most similar to that of *Lemur* among extant primates (fig. 9B).

The second digit of *Notharctus* is characterized by a relatively short metacarpal (table 5), the relative length of which is most similar to that of living lorises and *Propithecus* (fig. 10A). *Propithecus* and *Notharctus* differ from lorises in having an elongate second phalanx, which probably compensates somewhat for the short second metacarpal (fig. 10B). *Notharctus* also has a fourth metacarpal that is much longer than the third (table 5), resembling extant lorises and indriids in this respect (fig. 10A). Extant primates with a long fourth digit grasp arboreal substrates between the first and fourth digits using a "pincer grasp," which is well developed in lorises and indriids (Jouffroy and Lessertisseur, 1959; Jouffroy, 1975, 1993). Although Jouffroy et al. (1991) wrote that the short second metacarpal of *Notharctus* might be
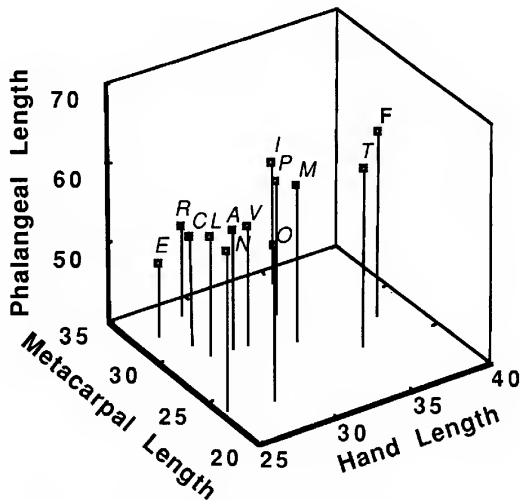
Fig. 8. Three-dimensional plot of mean species hand index values for a large sample of extant taxa and *Notharctus tenebrosus* (AMNH 127167). F = AMNH 127167, T = *Tarsius*, M = *Lepilemur*, P = *Propithecus*, I = *Indri*, O = *Perodicticus*, N = *Nycticebus*, V = *Varecia*, L = *Lemur*, A = *Aotus*, C = *Cebus*, R = *Presbytis*, and E = *Cercopithecus*. Hand length = hand length/forelimb length × 100, Metacarpal length = longest metacarpal length/hand length × 100, and Phalangeal length = length proximal + intermediate + terminal phalanx of longest digit/hand length × 100. Comparative data are from Jouffroy et al. (1991). Sample sizes are shown in figure 9B.

indicative of a behavioral specialization, Godinot (1992) remarked that the short second metacarpal might simply be correlated with an increase in fourth digit length (= ectaxony; see also Gregory, 1920). The combination of an elongate fourth metacarpal, short second metacarpal, and moderately elongate second and fourth proximal phalanges in AMNH 127167 (table 5) suggests that *Notharctus* was ectaxonic, and possessed a well-developed grasping hand for a variety of arboreal positional behaviors including clinging and climbing.

Comparisons with Other Eocene Primates

The ratio of first metacarpal length to third metacarpal length in AMNH 127167 has also been calculated for several early Tertiary adapiforms by Godinot (1992). His results show that *Adapis, Smilodectes,* and *Notharctus* all have a relatively short first metacarpal

whereas the European protoadapines, tarsiers, lorises, and platyrrhines have a longer first metacarpal relative to third metacarpal length (fig. 9B). The extant taxa possessing a relatively long first metacarpal (e.g., lorises, tarsiers, and platyrrhines) do not appear to us to share any particular locomotor or special manipulatory use of the hand. Hence, a long first metacarpal probably evolved independently in these extant taxa for different behaviors. We consider a relatively short first metacarpal primitive for euprimates, with a relatively longer pollical metacarpal having evolved independently in protoadapines, lorises, tarsiers, and platyrrhines for different prehensile behaviors.

Based on a broad survey of relative hand proportions across several groups of living primates by Jouffroy et al. (1991), extrinsic and intrinsic hand proportions of *Notharctus* approximate what we might expect to find in an early primate. These primitive features include (1) short metacarpals and long phalanges relative to hand length, (2) a moderately elongate thumb relative to hand length, and (3) short first metacarpal length relative to third metacarpal length. The first two features of *Notharctus* are shared with tarsiers and living strepsirhines, whereas the third feature is shared with *Adapis, Smilodectes,* and extant Malagasy primates. Although phalangeal proportions of the second and fourth rays in *Notharctus* do not mirror those of the metacarpals, intrinsic ray proportions of *Notharctus* are intermediate between those of living lemurids and indriids. The short second digit and long fourth digit are related functionally to pincer grasping specializations in these extant taxa. Intrinsic ray proportions of AMNH 127167 suggest that *Notharctus* lacked significant manipulatory capabilities of the thumb, but instead possessed a hand that was used primarily to securely grasp arboreal substrates during various postural and locomotor behaviors.

SUMMARY AND CONCLUSIONS

Quantitative and qualitative comparisons between AMNH 127167 and the hands of extant primates yield several important insights regarding the positional behavior of *Notharctus tenebrosus*. The elongate hand,

TABLE 5
Values Used to Calculate Relative Hand Proportions and Ratios for AMNH 127167
All measurements in millimeters.

Length measurement	Value
Extrinsic	
Forelimb (= humerus + radius + hand)	240.55
Hand (= carpus + metacarpus + phalanges)	84.83
Thumb (= first metacarpal + phalanges)	37.85
Metacarpal (= fourth metacarpal)	21.42
Phalangeal (= fourth proximal + intermediate + terminal phalanges)	52.78
Intrinsic	
Metacarpals	
I	12.48
II	16.65
III	21.0[a]
IV	21.42
V	19.06
Proximal Phalanges	
I	16.39
II	23.98
III	27.66
IV	28.51
V	25.47
Intermediate Phalanges	
II	16.08
IV	13.83[a]
V	13.94[a]
Terminal Phalanges	
I	8.98
II	8.14
III	9.38
IV	10.44
V	8.96

[a] Partially damaged.

phalanges, and moderately elongate thumb of AMNH 127167 indicate that it was clearly arboreal. The carpus of AMNH 127167 is quite similar in a number of features to that of predominantly pronograde taxa, such as *Varecia* and *Aotus*. These features include a relatively tall pisiform body, broad distal triquetral articular facet, broad capitate head, and radioulnarly reduced pollical carpometacarpal articular facet. The tall pisiform body of *Notharctus* increases the lever arm for m. flexor carpi ulnaris, which flexes the wrist from extended positions during the propulsive phase of quadrupedal strides (Whitehead, 1993). The radioulnarly expanded midcarpal joint articular surfaces of *Notharctus*

reduce joint stress when the wrist is subjected to compressive, weight-bearing loads during quadrupedal postures (Sarmiento, 1988). Finally, the pollical carpometacarpal articulation of *Notharctus* is not markedly expanded like that of lorisines and indriids—extant primates that use the thumb as a powerful grasping organ during acrobatic climbing and vertical clinging postures. Together, these features of the hand and wrist suggest frequent arboreal, pronograde habits for *Notharctus tenebrosus*. In addition, a handful of features (e.g., ray proportions) point to some orthograde clinging behaviors by *Notharctus* and may suggest an overall adaptation that, while most similar to pronograde taxa such
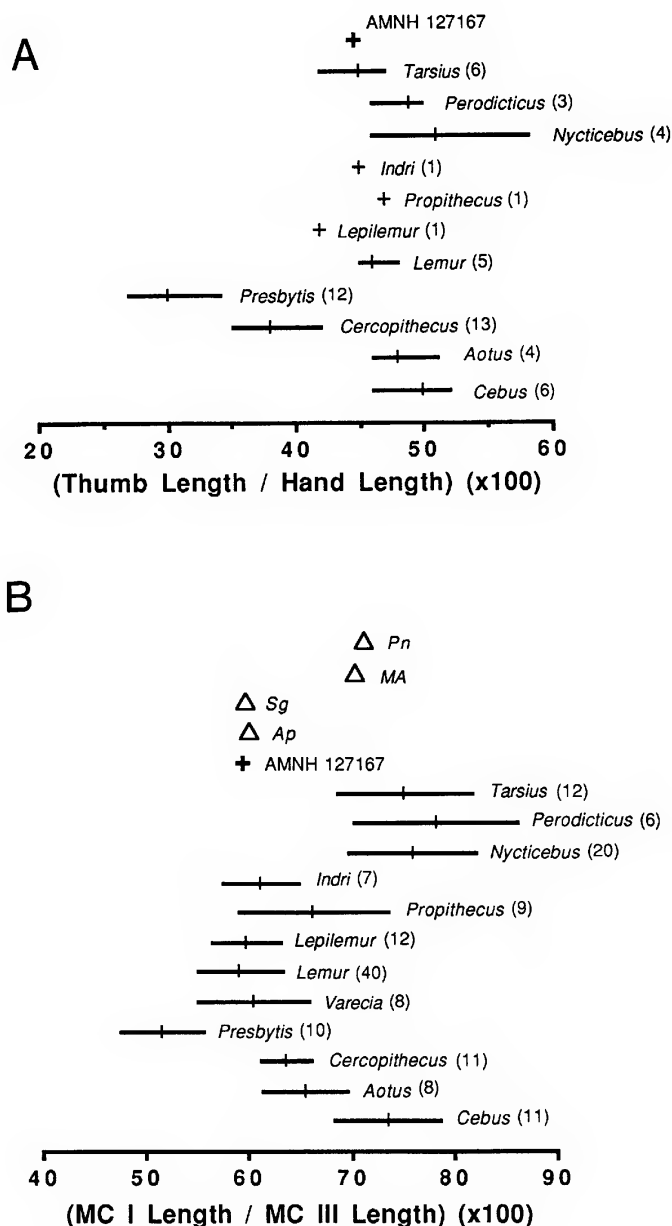
A

AMNH 127167
+

——+—— *Tarsius* (6)

——+— *Perodicticus* (3)

——————+—— *Nycticebus* (4)

+ *Indri* (1)

+ *Propithecus* (1)

+ *Lepilemur* (1)

—+— *Lemur* (5)

———+——— *Presbytis* (12)

——+——— *Cercopithecus* (13)

——+—— *Aotus* (4)

——+—— *Cebus* (6)

```
20      30      40      50      60
```

(Thumb Length / Hand Length) (x100)

B

△ *Pn*

△ *MA*

△ *Sg*

△ *Ap*

+ AMNH 127167

————+———— *Tarsius* (12)

————+———— *Perodicticus* (6)

————+———— *Nycticebus* (20)

——+—— *Indri* (7)

————+———— *Propithecus* (9)

——+—— *Lepilemur* (12)

——+—— *Lemur* (40)

——+—— *Varecia* (8)

——+—— *Presbytis* (10)

——+— *Cercopithecus* (11)

——+— *Aotus* (8)

————+—— *Cebus* (11)

```
40      50      60      70      80      90
```

(MC I Length / MC III Length) (x100)

Fig. 9. Univariate plots of (**A**) relative thumb length index and (**B**) relative pollical metacarpal length index for a large sample of extant primate taxa and *Notharctus tenebrosus* (AMNH 127167). Sample sizes in are in parentheses. Pn = *Pronycticebus neglectus,* MA = Messel adapiform, Sg = *Smilodectes gracilis.* Values for these fossil adapiforms are from Godinot (1992). Comparative data in (**A**) are from Napier and Napier (1967) and in (**B**) from Jouffroy et al. (1991).

as *Varecia* and *Aotus,* included some cling-ing behavior. This would be consistent with the body proportions and hip morphology of this taxon (Covert, 1986).

These new postcranial remains also allow us to test hypotheses regarding primate hand evolution. Our analyses support Godinot and Beard's (1991) conclusion that the earliest primate hands possessed both a narrow lunate and a tall pisiform body. Based on our

A

B
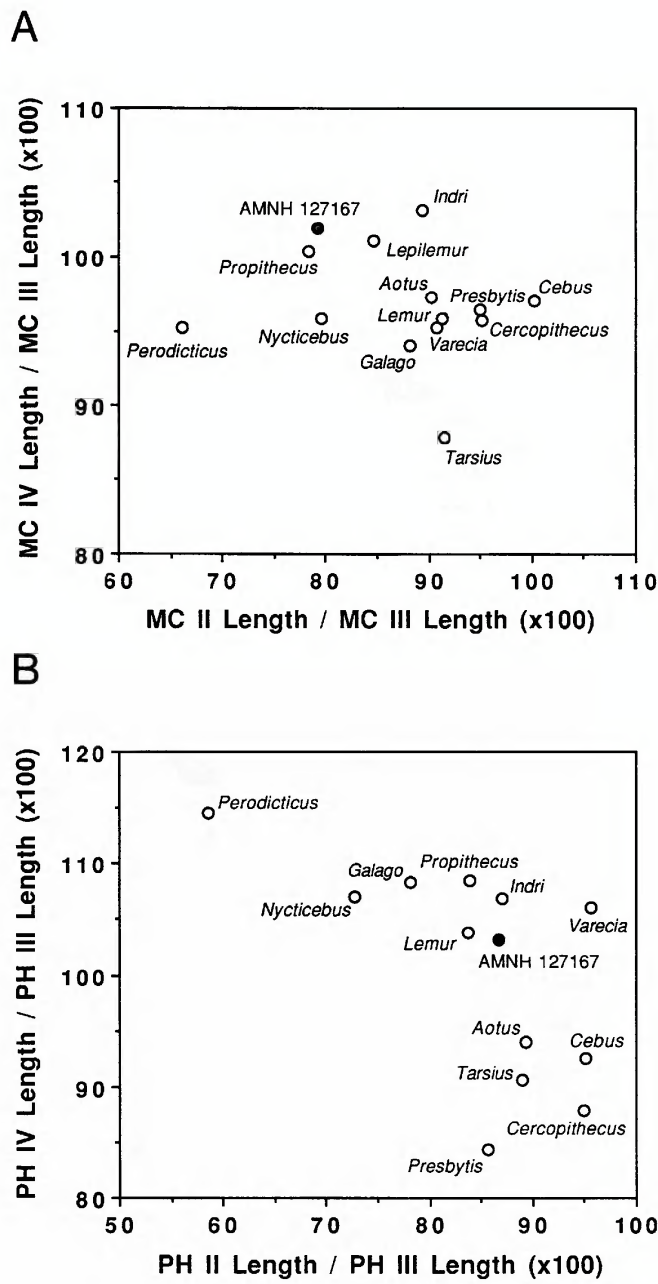
Fig. 10. Bivariate plots of (A) relative fourth metacarpal length against relative second metacarpal length and (B) relative fourth phalanx length against relative second phalanx length for a large sample of extant primate taxa and *Notharctus tenebrosus* (AMNH 127167). Sample sizes in (A) are the same as those shown in Figure 9A. Comparative data in (A) are from Jouffroy et al. (1991). Sample sizes in (B) are as follows: *Perodicticus* (2), *Galago* (3), *Nycticebus* (3), *Propithecus* (3), *Indri* (4), *Varecia* (4), *Lemur* (3), *Aotus* (3), *Cebus* (10), *Tarsius* (3), *Cercopithecus* (10), *Presbytis* (3).

comparisons between AMNH 127167 and the hands of extant and fossil primate taxa, we have expanded Godinot and Beard's (1991) description of the euprimate morphotype to include a moderately expanded capitate head, broad triquetrum, and pollical carpometacarpal articulation that is not markedly expanded. In terms of hand proportions, *Notharctus* resembles living strepsirhines and *Tarsius* in having relatively elongate phalanges, shorter metacarpals, and a shorter thumb compared to platyrrhine primates. We interpret the *Notharctus-Tarsius*-strepsirhine pattern as primitive for euprimates, as do Jouffroy et al. (1991), and consider the relatively longer thumb and metacarpals of platyrrhines to be derived.

The fact that several of the carpal features that we consider morphotypic for primates (e.g., large pisiform, broad triquetrum, broad capitate head) are functionally associated with habitual pronograde posture suggests to us that the common ancestor of primates practiced some form of pronograde locomotion. Given that very long hands and long manual phalanges also appear to be morphotypic for euprimates, manual grasping was likely a very important behavior for early primates living in an arboreal environment. The elongate manual and pedal digits of these early primates are well suited for a number of biological roles including climbing and walking between arboreal supports of variable size and orientation. Based on our reconstruction of the euprimate hand, we agree with Dagosto (1988: 51) that "the common ancestor of all known euprimates was a type of arboreal quadruped in which leaping and climbing were the predominant methods of displacement" (e.g., "grasp-leaping," sensu Szalay and Dagosto, 1980).

Even though the hand of *Notharctus* shows a number of features that we interpret as being primitive for euprimates, AMNH 127167 also displays several features quite different from those of the extant and fossil primates studied. These features include an exceptionally small trapezium relative to carpal size, a very large trapezoid, and a short second metacarpal. These three features could be correlated with a greater commit-

ment to palmigrade locomotion by *Notharctus* beyond that practiced by the euprimate common ancestor. These morphologies might also be related to "pincer grasping" arboreal substrates between the first and fourth digit, resulting in preferential loading along the long axis of the second ray. Nevertheless, the hand of *Notharctus* shares a number of features with the hands of both haplorhine and strepsirhine primates. This new information sheds light upon the manner in which both groups have diverged in hand structure and function relative to the ancestral primate morphotype.

ACKNOWLEDGMENTS

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